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Use of the Barker model in an experiment examining covariate effects on first-year survival in Ross's Geese (*Chen rossii*): a case study

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ABSTRACT *The Barker model provides researchers with an opportunity to use three types of data for mark-recapture analyses—recaptures, recoveries, and resightings. This model structure maximizes use of encounter data and increases the precision of parameter estimates, provided the researcher has large amounts of resighting data. However, to our knowledge, this model has not been used for any published ringing studies. Our objective here is to report our use of the Barker model in covariate-dependent analyses that we conducted in Program MARK. In particular, we wanted to describe our experimental study design and discuss our analytical approach plus some logistical constraints we encountered while conducting a study of the effects of growth and parasites on survival of juvenile Ross's Geese. Birds were marked just before fledging, alternately injected with antiparasite drugs or a control, and then were re-encountered during migration and breeding in following years. Although the Barker model estimates seven parameters, our objectives focused on annual survival only, thus we considered all other parameters as nuisance terms. Therefore, we simplified our model structures by maintaining biological complexity on survival, while retaining a very basic structure on nuisance parameters. These analyses were conducted in a two-step approach where we used the most parsimonious model from nuisance parameter analyses as our starting model for analyses of covariate effects. This analytical approach also allowed us to minimize the long CPU times associated with the use of covariates in earlier versions of Program MARK. Resightings made up about 80% of our encounter history data, and simulations demonstrated that precision and bias of parameter estimates were minimally affected by this distribution. Overall, the*

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main source of bias was that smaller goslings were too small to retain neckbands, yet were the birds that we predicted would have the lowest survival probability and highest probability for parasite effects. Consequently, we considered our results conservative. The largest constraint of our study design was the inability to partition survival into biologically meaningful periods to provide insight into the timing and mechanisms of mortality.

1 Introduction

The study of factors influencing survival in wild animals can be confounded by the difficult task of following marked individuals through time and space, particularly if those animals undergo long-distance movements and so are difficult to re-encounter. For such species, researchers may still obtain encounter data but over large geographic areas and, depending on the marker types, from several sources, including recaptures, resightings, and recoveries. These three types of encounter data can be incorporated into study designs and analysed with the Barker model (Barker, 1997; Barker & White, 1999). This model was originally developed to separate true survival from fidelity to the recapture site, which are confounded in estimates of apparent survival (phi), by including data from resightings and recoveries away from the recapture area (Barker, 1997; Barker & White, 1999). As such, by allowing use of resighting data, the Barker model is an extension of Burnham's (1993) model for joint analysis of recapture and recovery data (Barker & White, 1999). Herein, we describe an application of the Barker model for examining the effects of multiple covariates on survival in juvenile Ross's Geese (*Chen rossii*). Published information for this model has become available only since 1997 (Barker, 1997; Barker & White, 1999) and, to our knowledge, no study using this model has been published for marked birds.

Ross's geese are a highly mobile species with long-distance migration between breeding grounds in the central Canadian Arctic and wintering termini in southern North America, including California, New Mexico, Texas and Mexico (Bellrose, 1980). This species nests with Lesser Snow Geese in colonies that occasionally exceed 600 000 geese. These large populations may be degrading feeding areas (Jano *et al.*, 1998; Slattery, 2000), which has implications for growth and survival of the young. At one large colony, food availability increases farther from the nesting area (Slattery, 2000), possibly related to foraging activities of geese. Broods disperse variable distances across the food gradient, and goslings raised at more distant sites are structurally larger and heavier for their body size than those reared nearby. Because structural size or weight of young at fledging or weaning can influence first-year survival in some species of birds and mammals (Owen & Black, 1989, 1991; Linden *et al.*, 1992; Schmutz, 1993; Sauer & Slade, 1987; Wauters *et al.*, 1993), we predicted that post-fledging juvenile survival may be affected by brood dispersal. In addition, gastric parasites can influence digestive efficiency (Munger & Karasov, 1989), which may have energetic consequences during periods of nutritional stress. Little is known, however, about how growth affects survival in fledged Ross's Geese and, more importantly, how body size, condition, or other gosling characteristics near fledging interact with energetic constraints, such as gastric parasitism, to influence the probability of first-year survival. We used a formal experiment to examine the effects of hatch date, growth, brood dispersal, and gastric parasites on first-year survival. Therefore, our analytical objectives were not only to derive estimates of survival for geese with different group covariates (e.g. control versus treatment for parasites), but also to examine survival probability

relative to individual covariates (e.g. indices of individual quality such as body size) and the interaction between group covariates and individual covariates. Full results are presented in Slattery (2000) and Slattery & Alisauskas (in preparation). Because this study is among the first to employ the Barker model for experimentally examining the interactive effects of group and individual covariates on survival, our objectives here are to discuss constraints and solutions we encountered during our research. We believe this case study will aid the design and analysis of conceptually similar projects.

2 General marking and re-encounter procedures

Goslings were captured on the breeding grounds at Karrak Lake, Nunavut (67°14′N, 100°15′W), within about < 10 days of fledging, and weighed, measured and marked with individually-coded plastic neck bands and aluminium leg bands (Slattery, 2000). The head size of goslings varied considerably during marking, and so to reduce bias in survival estimates due to collar loss (Alisauskas & Lindberg, this issue), goslings that were too small to retain collars were not marked as part of this study. This constraint resulted in a marked sample of 69% ($n = 512$), 89% ($n = 813$), 52% ($n = 235$) and 72% ($n = 735$) of goslings we captured from 1994 to 1997, respectively. During marking, goslings were injected with an antiparasite drug (Experiment 1: Ivermectin (a nematocide, Oksanen & Nikander, 1989) in 1994-1995 or Experiment 2: Droncit (a cestocide, Andrews *et al.*, 1983) in 1996-1997) or physiological saline as a control. Our efficacy studies demonstrated that these drugs either substantially reduced or eliminated three of four species of gastro-intestinal parasites (Slattery, 2000).

Marked birds then were resighted during migration and nesting, recaptured during subsequent marking operations on the breeding grounds, or shot by hunters. Nesting observations were only conducted at Karrak Lake, which contains about 40% of the Ross's geese nesting in the central Canadian Arctic (Kerbes, 1994). Birds were followed for up to 5 years after marking, with last recaptures in 1999. We considered birds that were recaptured or resighted during the breeding season as recaptured. Therefore, the recapture period was from about 25 May-20 August and a resighting/recovery period (interval i, $i + 1$) was from about 21 August-24 May.

During this study, we obtained 110 recaptures, 2714 resightings and 147 recoveries of marked birds between September 1994-August 1999. Of resightings, 1122 were unique within intervals i, $i + 1$. We re-encountered 36% ($n = 831$) of marked birds during the study.

3 Preliminary statistical analyses

We used Principal Component Analyses (PCA) to examine the correlation matrix of midwing, tarsus and body lengths and used the first principal component (PC1) as our index of structural size (Reyment *et al.*, 1984). We then indexed body condition by taking residuals of body mass regressed against body size (Piersma & Davidson, 1991). Goslings were of unknown hatch date, so we used the ninth primary length as an index of age and the ninth primary length corrected for time since peak hatch as an index of hatch date (see Slattery, 2000, for a discussion). Other analyses (Slattery, 2000) suggest that goslings can compensate for gastric parasitism prior to fledging, so gastric parasites likely did not interact with feather

growth to confound age analyses. Marked and unmarked goslings were pooled for preliminary analyses. We marked birds over a 10-14 day period, which may have caused observer-induced variation in gosling size because goslings were still growing during the marking period. Therefore, we standardized gosling body size by regressing PC1 against ninth primary and used residual size for subsequent analyses, i.e. goslings were corrected to a common age (Slattery, 2000; Slattery & Alisauskas, in preparation). These corrections were unnecessary for body condition. In addition, we examined dependence of our hatch date index on dispersal distance using a simple linear regression to explore collinearity between these variables. We concluded that although earlier-hatched goslings tended to be captured farther from the colony in 2 of 4 years, distance explained $\leqslant 5\%$ of the variation in gosling age (Slattery, 2000; Slattery & Alisauskas, in preparation) and so for our purposes we considered the relationship essentially random. We also explored collinearity among size or condition and distance and hatch date.

4 Sources of bias

Before proceeding with analyses, we needed to explore limitations within our study design and field logistics to better understand how these limitations might influence interpretation of our results. First, our marked sample was potentially biased because the smallest goslings, hence those thought to be least likely to survive (Sedinger *et al.*, 1995; van der Jeugd & Larsson, 1998), could not be marked with neckbands. This logistical limitation resulted in a truncated sample population, which may have biased survival estimates high and reduced our ability to detect differences between parasite treatment categories, especially if parasites interacted with gosling size. Note, however, that level of parasite infection and goslings size or condition were not correlated (Slattery, 2000). Our partial solution to this dilemma was to compare body size, condition, and hatch date between marked ($n = 2{,}295$ goslings) and unmarked ($n = 824$) samples using analyses of variance, treat our results for survival estimates as conservative, and hypothesize about survival of the unmarked birds based on results for the marked birds. Years were analysed separately and, in almost all cases, unmarked goslings were structurally smaller, in poorer body condition, and hatched later than marked birds.

A second constraint to our analyses was that neckbands might have interacted with gosling survival. Neckbands are useful tools for following individuals across time and space, but they also may reduce survival (Johnson *et al.*, 1995; Alisauskas & Lindberg, this issue). Because we were not interested in actual survival estimates, but rather the relative differences between treatment groups and the general relationship between survival and covariates, we were willing to accept this potential experimentally induced reduction of true survival estimates.

5 General modelling procedures

This section overviews our modelling procedures to provide context for discussion of problems we encountered during analyses. See Slattery (2000) or Slattery & Alisauskas (in preparation) for detailed methods.

We examined variation in first-year survival due to drug treatment (i.e. parasites) and the following individual covariates: sex, distance captured from the colony, hatch date, structural size, body condition, size $\times$ condition, and treatment $\times$ covariate interactions. Although sex is typically modelled as a group covariate, we

modelled the variable as an individual covariate to reduce the number of parameter index matrices (PIMs, White & Burnham, 1999). This format should not have altered results (Franklin, 1999). Interactions with treatment were specified in the design matrix by multiplying the binary treatment code by individual covariates (Franklin, 1999). Program MARK cannot calculate interactions among individual covariates, and so we input the size × condition interaction by creating a new covariate by multiplying structural size and body condition (Franklin, 1999) in Microsoft Excel. Finally, although many interactions among individual covariates could have been included in our analyses, we chose to reduce the analytical complexity of our models by only including size × condition, which was the most biologically relevant interaction for examining effects of growth on survival and the most likely to further interact with parasitism. Covariate effects were only examined for juvenile age classes.

The Barker model has seven basic parameters, which include: S_i—survival probability from i to $i+1$, p_i—recapture probability given alive at i, r_i—recovery probability given dead, i, $i+1$, R_i—resight probability given alive, i, $i+1$, R'_i—resight probability in i, $i+1$ before death in i, $i+1$, F_i—fidelity probability to the capture area, and F'_i—temporary emigration from recapture area (Barker & White, 1999). We were only interested in examining covariate effects on survival, and so used a two-step approach to reduce these Barker parameters. This approach simplified our models and helped circumvent logistical constraints associated with the use of covariates (see below). Goodness-of-fit testing was used to calculated $\hat{c}$ at the beginning of each step using 500 iterations of parametric bootstrapping in Program MARK (White & Burnham, 1999), and subsequent model selection was based on AIC_c or $QAIC_c$ as appropriate (Burnham & Anderson, 1998). In our first step, we began with full time and treatment dependency in our saturated model, then used a backwards stepwise approach to reduce parameters in the following order: F'_i, F_i, R'_i, R_i, r_i, p_i and S_i. Two age-classes (adults and juveniles) were considered only for survival, which further reduced the analytical complexity of our models. We then considered the most parsimonious model from this stage as our starting model for the next step. In our second step, covariates and interactions were included in models but only for survival in juvenile age classes. Model selection was as above. Inclusion of the fully saturated survival term, i.e. with covariate effects on S, when selecting for the most parsimonious model for nuisance parameters may have provided more robust model selection, but our two-step approach should not have altered our conclusions about relationships between survival and covariates.

We went to considerable efforts to simplify model structure before proceeding with model selection for two main reasons. First, the Barker model is parameter-rich, and so requires considerable data to estimate multiple parameters for very complex models. We did not have sufficient data and, more importantly, analysis of such complex models was not our *a priori* intent, so we simplified selection of six Barker parameters (F'_i, F_i, R'_i, R_i, r_i, p) while only evaluating treatment and time variation, and maintaining biological complexity for the parameter of interest, survival. Secondly, inclusion of covariates in the data set exponentially increased computer-processing time, even if those covariates were not specified in the model. Exploratory analyses suggested that the presence of covariates prevented summarization of unique encounter histories before analysis, and so Program MARK may have considered each record as a unique encounter history. This problem has subsequently been corrected by Gary White (see Program MARK

Website, http://www.cnr.colostate.edu/%7Egwhite/mark/mark.htm). Therefore, we simplified models while considering trade-offs in the amount of biological information described by a model and our logistical constraints in analysing that model.

Finally, approximately 80% of our encounter data were resightings, while recaptures comprised 8%. This distribution among encounter categories may have affected the precision and bias of parameter estimates. Consequently, we conducted simulations in Program MARK using the Barker model in which resightings comprised 5%, 25%, 50%, 75% and 95% of the encounter data and examined effects on point estimates and standard error width. These proportions were created by altering p and R, while keeping S, r, R', F and F' constant at values based on the above analyses (0.75, 0.06, 0.12, 1 and 0, respectively). The resulting distribution of data among encounter categories was verified in SAS before proceeding with simulations in Program MARK. We then used the identity matrix and link function for both true and estimation models, $S(.)p(.)r(.)R(.)R'(.)F(.)F'(.)$, and ran 1000 iterations, with five time intervals and 100 releases per interval for each iteration. These simulations demonstrated that the proportion of resightings in encounter histories did not affect the precision or bias of survival estimates (Fig. 1). Indeed, only the mean of R' increased slightly after 75%, while precision decreased as the proportion of resighting data increased, particularly at the 95% level (Fig. 1). Consequently, although we were unable to simulate the effects of covariates, we concluded that the large proportion of resightings in our encounter histories did not affect our estimates of survival.

6 Examination and interpretation of results

When using covariate-based models, Program MARK only provides a single point estimate of survival probability based on either mean covariate values or the covariate values of the first record in the data set. Therefore, to examine fully the relationship between survival covariates, i.e. the effect size, additional calculations are necessary. We used two approaches to plot and interpret our results based on the most parsimonious model, and the beta estimates and link function equation for that model (Cooch, 1999; Franklin, 1999). Program MARK uses linear modelling to estimate parameters, and beta terms are essentially slope estimates for link function equations (Cooch, 1999). Therefore, as a first step, we examined precision of those beta terms, i.e. 95% confidence intervals, plus their sign, to help further interpret covariate effects. However, although the sign of beta terms alone may indicate the general direction of the relationship, it does not reveal the biological effect size. Such examination requires a graphical approach.

The first graphical approach we used examined individual covariate effects on survival in a continuous context. Link function equations were used to compute survival probability across a range of values for the focal covariate, while holding other covariates constant at their mean values. We considered these calculations as conceptually analogous to examining independent, i.e. additive, effects of covariates using type III sums of squares in general linear models (Hatcher & Stepanski, 1994). Survival probability was estimated for each drug treatment at the following five values of the focal covariate for the marked population: minimum observation, maximum observation, mean, and ± 1 standard deviation, separately for each year (Fig. 2).

We next examined variation in survival in a categorical context to further

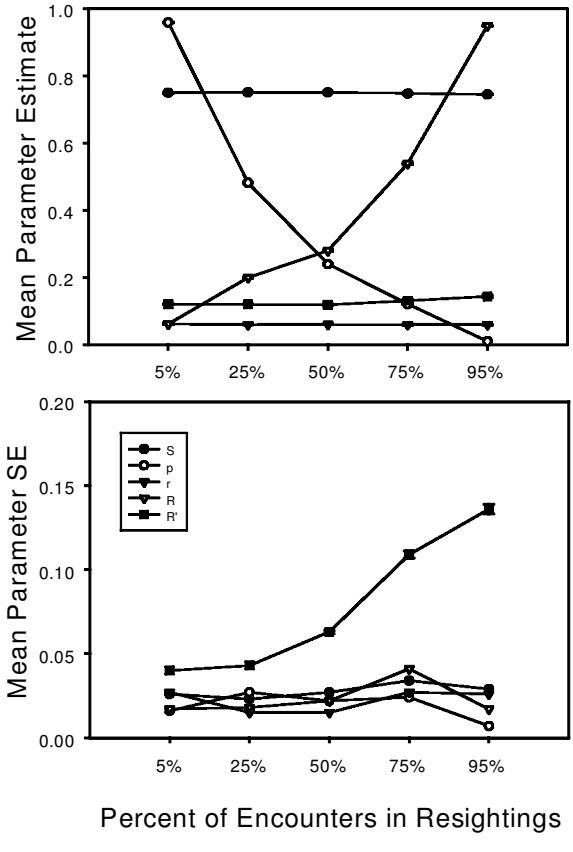

FIG. 1. Effects of variation in resighting data as a proportion of total encounters on precision and bias in parameter estimates. Only relative numbers of resightings and recoveries were altered when creating simulated data. See text for a description of simulation techniques. Results shown are mean and standard error for each point. Deviation from truth was minimal for all parameters, while precision (standard error, SE) slightly decreased with increasing percent resightings only for R'. Barker parameter key (truth): S—survival probability (0.75), p—recapture probability (0.96, 0.48, 0.24, 0.12, 0.01), r—recovery probability (0.06), R—resighting probability given alive during interval i to $i+1$ (0.07, 0.20, 0,28 0.54, 0.95), R'—resighting probability given died during interval i to $i+1$ (0.12). Fidelity parameters were fixed and so are not presented.

interpret interactions and compare the relative effects of covariates. We considered this technique to be conceptually similar to resolving interactions in a regression context, e.g. breaking up the interaction and re-examining the data. However, we admit that by collapsing continuous relationships into categorical relationships, we are trading off some biological resolution for a more easily interpreted format. We used ± 1 standard deviation as the input values for covariates, creating categories based on the mean (above and below), and varied all coviariates simultaneously in link function equations. For example, our most parsimonious model in the Droncit experiment included an interaction between structural size, body condition and treatment (Slattery, 2000; Slattery & Alisauskas, in preparation). To examine this complex interaction further, we used the link function equation to calculate survival in four size $\times$ condition categories within each drug treatment (Fig. 3). Finally, to examine the relative importance of structural size, condition and hatch date, we similarly calculated survival for eight combinations of these covariates, but only for

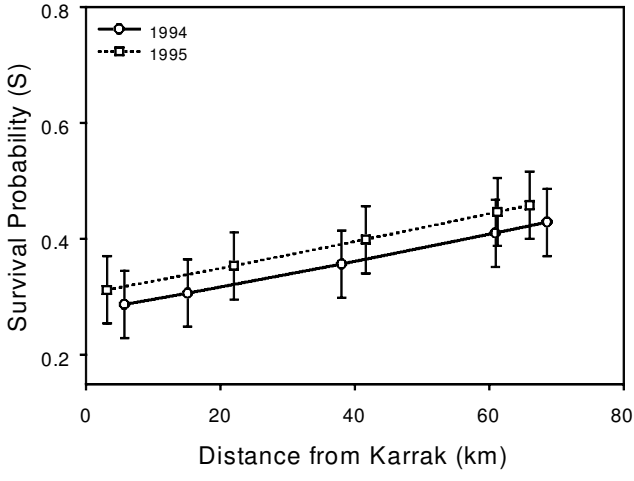

FIG. 2. Examination of continuous covariate effects on survival. Program MARK only supplies an estimate of survival based on one data point. This graphical technique permits better interpretation of biological effect size. Shown is the effect of distance that Ross's goslings on brood rearing areas were captured from Karrak Lake on annual juvenile survival in the Ivermectin study, 1994-1995 ($n = 512$ and 813 goslings, respectively). Data points are minimum value, mean—1 standard deviation (sd), mean, mean + 1 sd, and maximum value of x-axis within each year. Error bars are standard errors. From Slattery (2000).

the control (saline) group (Fig. 4). This latter graphical examination indicated that hatch date was the most important covariate that we measured, which corresponded to model selection results where the $QAIC_c$ or AIC_c values increased by about 18 units when hatch date was removed from the best model, but only by about 3 units when one of the other covariates was removed. Although the AIC examination is a necessary approach for these types of analyses, addition of the graphical approach permits better visualization and interpretation of the biological effects of each covariate on survival.

7 General discussion

The Barker model and Program MARK allowed us to use multiple sources of encounter data to conduct a unique experiment on survival in juvenile birds. The Barker model can also provide greater precision in parameter estimates, provided resighting probability is high. This increase would only be obtained by substantially greater effort in marking and re-encountering birds when analyses rely on one type of data (Barker & White, 1999). Such constraints on sample size are real considerations for researchers, particularly for animals with long-range dispersal ability or when subsequent recaptures are logistically challenging, and so the Barker model provides the researcher with greater flexibility in study design.

For our experiment, we were interested in biological constraints on survival and considered the remaining Barker parameters as nuisance variables that we wanted properly structured for estimation of survival. Although we might have obtained better model structure by including individual covariate effects on nuisance parameters, we did not include such models because we were not making *a priori* predictions about covariate effects on nuisance parameters and wanted to avoid

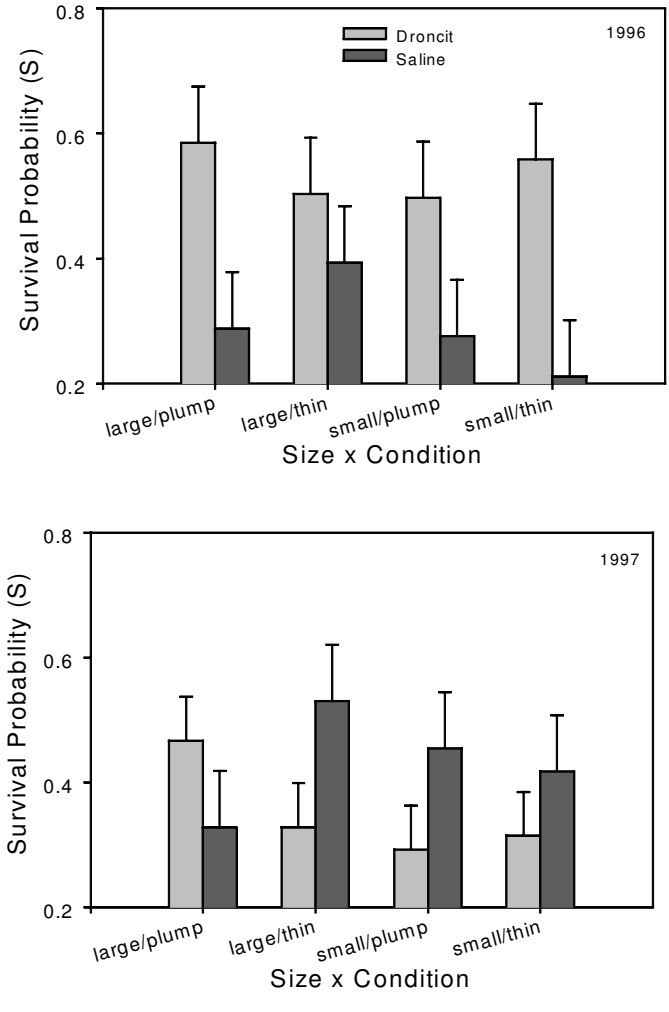

FIG. 3. Example of the graphical technique used to examine interaction among covariates. Three-way interaction shown is for structural size × body condition × treatment effects on annual survival of Ross's goslings in the Droncit study. From Slattery (2000).

data dredging in our analyses. However, subsequent exploratory analyses for covariate effects on R indicated that inclusion of these effects increased AIC_c values by over 64 units, suggesting that our approach was robust.

One of the main limitations of our study design and analyses using the Barker model was the inability to partition survival probability into seasonal components. The Barker model estimates survival from i to $i + 1$, which was one year for this study. However, we suspect that most migration mortality occurs during the first leg of migration when goslings are flying between breeding grounds and migratory staging areas in the Canadian prairies (Francis *et al.*, 1992). This flight is about 1800 km and little food is available at this time, so goslings probably rely primarily on energy reserves stored in the arctic. Therefore, constraints on premigratory fattening could have resulted in mortality during this long flight. In addition, the cestode species that we observed disappeared from the parasite community by fall (Neraasen, 1970; Slattery, unpublished data), which suggests that the cestode

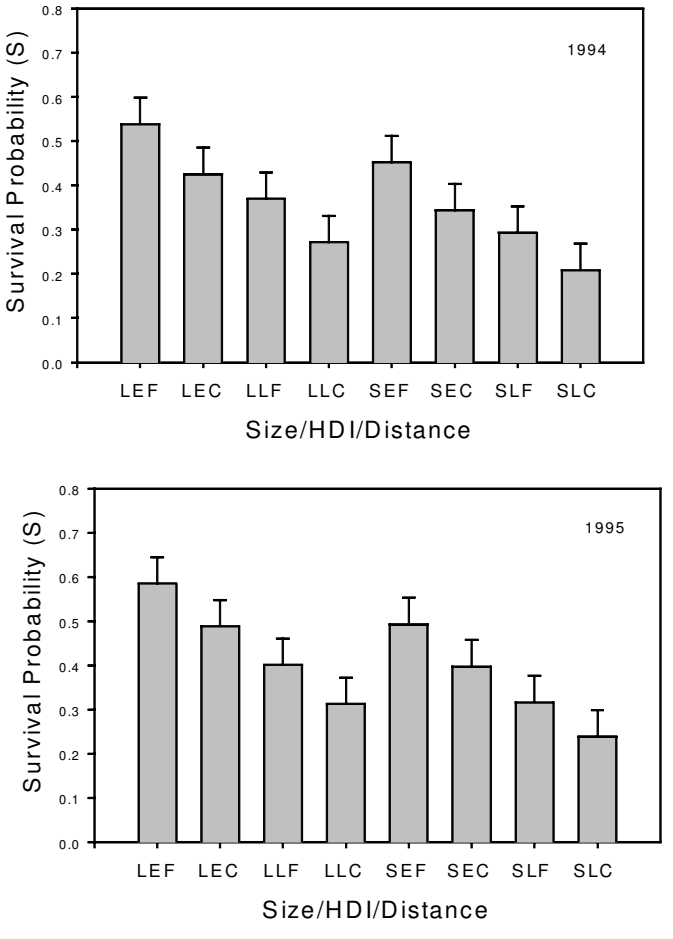

FIG. 4. Visual analysis of relative biological importance of covariates. This technique supplements the AICc approach and more clearly demonstrates biological effect size. Shown are relative importance of structural size, hatch date index (HDI), and dispersal distance (distance) on estimates of annual survival in 1994 and 1995. Values used to estimate survival were mean ± 1 sd for each covariate. Covariates are coded by one letter in the following order: size-HDI-distance. Codes: size—L = large, S = small; HDI—E = early-hatched, L = late-hatched; distance—C = close, F = far; e.g. LLF = large, late-hatched goslings reared far from Karrak Lake. From Slattery (2000).

effects on survival that we observed only occurred between marking and arrival on prairie staging areas. The ability to partition survival among seasons would have given us greater insight into the timing and mechanisms of mortality. Although further exploration of treatment effects on Barker parameters r and R' may yield additional insights, Cormack-Jolly-Seber models may have allowed us to partition survival across biologically significant periods (Schmutz & Ely, 1999). Therefore, although the Barker model is a great addition to capture-mark-recapture analysis, we are exploring the applicability of other techniques to our data set to answer additional questions.

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